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Small invertebrate consumers produce consistent size spectra across reef habitats and climatic zones

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Changes in invertebrate body size-distributions that follow loss of habitat-forming species can potentially affect a range of ecological processes, including predation and competition. In the marine environment, small crustaceans and other mobile invertebrates ('epifauna') represent a basal component in reef food webs, with a pivotal secondary production role that is strongly influenced by their body size-distribution. Ongoing degradation of reef habitats that affect invertebrate size-distributions, particularly transformation of coral and kelp habitat to algal turf, may thus fundamentally affect secondary production. Here we explored variation in size spectra of shallow epifaunal assemblages (i.e. the slope and intercept of the linear relationship between log abundance and body size at the assemblage level) across 21 reef microhabitats distributed along an extensive eastern Australian climatic gradient from the tropical northern Great Barrier Reef to cool temperate Tasmania. When aggregated across microhabitats at the site scale, invertebrate body size spectra (0.125–8 mm range) were consistently log-linear (R^2 ranging 0.87–0.98). Size spectra differed between, but not within, major groups of microhabitats, and exhibited little variability between tropical and temperate biomes. Nevertheless, size spectra showed significant tropical/temperate differences in slopes for epifauna sampled on macroalgal habitats, and in elevation for soft coral and sponge habitats. Our results reveal epifaunal size spectra to be a highly predictable macro-ecological feature. Given that variation in epifaunal size spectra among groups of microhabitats was greater than variation between tropical and temperate biomes, we postulate that ocean warming will not greatly alter epifaunal size spectra directly. However, transformation of tropical coral and temperate macroalgal habitats to algal turfs due to warming will alter reef food web dynamics through redistribution of the size of prey available to fishes.

Keywords: coral reef, epifauna, food web, macroalgae, macrofauna, meiofauna

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Introduction

Global climate change and local anthropogenic pressures are driving collapse of natural habitats within many ecosystems. Examples include direct impacts of clear-felling on forests (Nepstad et al. 1999), effects of climate-altered fire regimes on forests (Enright et al. 2015) and savannas (Scheiter et al. 2015), and coastal modifications to wetlands (Mitsch and Hernandez 2013). Widespread loss of key biogenic habitats in reef systems – such as corals (Hughes et al. 2018, Stuart-Smith et al. 2018) and kelp forests – is occurring due to direct (Krumhansl et al. 2016, Vergés et al. 2016, Wernberg et al. 2016) and indirect impacts of ocean warming (Ling 2008, Bates et al. 2017), and exacerbated by anthropogenic activity such as dredging (Lenihan and Peterson 2004), trawling (Kaiser et al. 2002), and eutrophication and pollution from land-based run-off (Bell 1992, Wolff et al. 2018). While habitat transformation is readily observable, understanding the ecological consequences requires knowledge of how food webs are altered by changes in habitat, particularly for taxa that are strongly linked to particular habitat types. Shifts in body size-distributions of important prey taxa can be an important mechanism of ecological change, as animal size-distribution affects prey availability to different predators (Ling et al. 2009, Kramer et al. 2015).

Small mobile epifaunal invertebrates ('epifauna') play a pivotal role in shallow food webs by trophically linking primary producers to higher carnivores (Edgar and Shaw 1995, Newcombe and Taylor 2010, Kramer et al. 2013). Impacts of widespread habitat change on epifauna, as well as any direct effects of climate change, will thus affect higher trophic levels including fishery resources (Connolly 1994, Edgar 1999), which are more directly valued by society. However, little information exists on how basal food web dynamics vary among reef habitat states or in different climate regimes (Edgar 1993, Kramer et al. 2017). Consequently, the extent that phase-shifts among reef habitats and changing ocean climates affect the basal epifaunal trophic level, and thus the availability of food resources to higher trophic levels, remains speculative.

Epifaunal taxonomic composition varies with the structure of habitats (Stella et al. 2010, Marzinelli et al. 2014), and habitat structure can overshadow the influence of environmental variation on the composition of epifaunal taxa along a broad latitudinal gradient (Fraser et al. 2020a). This suggests that on any given patch of reef, changing habitats may have greater impacts on food availability for invertivores than changing temperatures. Significant differences in the composition, biomass and production of epifaunal crustacean assemblages were recently identified between a temperate and a tropical location, on habitats of similar structure (Kramer et al. 2017), suggesting potential for complex interactive effects between habitat and temperature. However, availability of epifaunal invertebrates as prey for invertivores is influenced by more than taxonomic composition.

Benthic invertivores show strong size-specific prey selection (Edgar and Aoki 1993, Kramer et al. 2015), hence knowledge of body size distributions within epifaunal assemblages is critical for understanding the availability of food resources for different invertivore species. When the frequency distribution of individual body sizes is plotted for a given trophic group (often using a linear model – referred to as the size spectrum (White et al. 2007, Edwards et al. 2017)), the abundance of animals typically declines with increasing body size (Peters and Wassenberg 1983, Marquet et al. 1990, Damuth 1991). Hence, size spectra are generally negatively sloped, and the steepness of the slope indicates variation in the relative contributions of larger versus smaller animals (Trebilco et al. 2015). Size spectra slopes tend to be consistent in undisturbed aquatic systems (Sheldon et al. 1972, Trebilco et al. 2013), with inconsistencies observed when predator abundance is overestimated or when energy subsidies are provided from non-local sources (Trebilco et al. 2013). Explanations of variation in size spectra slopes are generally based on a few ecological principles, for example size-selective predation pressure from outside the modelled community, whereby larger body-sizes are generally more readily consumed, leading to steeper size spectra (Rassoulzadegan and Sheldon 1986). Steeper size spectra may also be related to inefficiencies in the transfer of energy from prey to predators within the modelled community (Lindeman 1942, Trebilco et al. 2013). Variation in the primary production and ecological state of the system may also affect community size spectra, for example the slopes of plankton size spectra in freshwater lakes were found to decrease from oligotrophic to eutrophic conditions (Sprules and Munawar 1986).

To date, no published studies have investigated the size spectrum of epifaunal assemblages on structurally diverse habitats among multiple locations extending from tropical to temperate reefs. A recent study comparing biomass size spectra of infaunal communities across a latitudinal gradient of 60–81°N found no significant latitudinal variation (Mazurkiewicz et al. 2020). However, other related ecological attributes clearly vary with latitude (Poulin and Hamilton 1995, Fisher et al. 2010), including the abundance and diversity of potential epifaunal predators (Ebeling and Hixon 1991, Edgar et al. 2017). The trophic state of reef systems also tends to differ substantially with latitude; low latitude coral reefs are typically oligotrophic systems (McClanahan et al. 2002), while high-latitude macro-algae dominated rocky reefs are typically more eutrophic (Burkepile and Hay 2006). Given these latitudinal trends, and the strong compositional differences in epifauna driven by habitat structure (Fraser et al. 2020a), the epifaunal size spectrum could potentially vary between tropical and temperate ecosystems and with habitat structure.

Here we investigate variation in the abundance size spectrum of epifaunal assemblages at 11 diverse shallow reef locations in eastern Australia. This region is a known hotspot of ocean warming (Poloczanska et al. 2007, Babcock et al. 2019), with climate-driven habitat transformation observed to extend from the Great Barrier Reef (Stuart-Smith et al. 2018) to subtropical coral reefs (Kim et al. 2019) to warm-temperate reefs off south-eastern mainland Australia

(Marzinelli et al. 2014) and cool-temperate rocky reefs off Tasmania (Johnson et al. 2011, Wernberg et al. 2011). Specifically, we test the hypothesis that epifaunal abundance size spectra will vary as a result of interactive effects between habitat type and climatic zone (i.e. tropical versus temperate). Our overarching goals is to shed light on the likely consequences of ongoing warming and habitat transformation on this basal component of reef ecosystems.

Material and methods

Study area and field sampling

Shallow reefs were sampled at 11 locations along the eastern seaboard of Australia, from southern Tasmania (43.3°S) to Lizard Island in the northern Great Barrier Reef (14.7°S) (Fig. 1). Sampling locations spanned a mean annual temperature gradient of 14.3–27.1°C. A total of 148 samples of benthic microhabitats (Table 1, 3) and associated epifauna were collected in September and October 2015, and over a 22 month period from January 2017 to November 2018. At each location, between 2 and 11 sites were sampled with numbers of sites and samples depending on logistic constraints and the timing of each sampling trip. Sites were separated by a minimum distance of 2.5 km.

Site sampling involved SCUBA-based collection of a subset of 20 different microhabitat types concurrently with associated epifaunal invertebrates. The distinction between microhabitats was based on a combination of taxonomy and morphology, as applied in previous studies to classify seabed habitat types (Cresswell et al. 2017) and by the CATAMI scheme (Althaus et al. 2015), which provides a national standard for Australian benthic habitat classification. Microhabitats were selected for sampling as they were sighted, with a minimum distance of 5 m between selected samples. The presence of different microhabitats at each site determined which were collected, with efforts made to sample one replicate of each microhabitat available at each site. Each microhabitat was identified as belonging to one of four major habitat groups based on taxonomy and morphology (Table 1).

Following Fraser et al. (2020a), prior to collection, a 25 × 25 cm grid-subdivided quadrat was placed over the selected microhabitat and photographed to quantify the seabed area covered by the microhabitat. Samples were enclosed and sealed within plastic bags. Macroalgae, sponges and soft corals were removed with a sharp knife; branching hard corals were removed with a chisel and rubber mallet; coral rubble was collected by hand. Epifauna associated with turfing algae and massive corals, which could not easily be removed for sampling, were collected using a venturi-powered vacuum with a 500 μm mesh bag secured over the outlet. The entire planar area within the quadrat was swept in suction samples. The mesh bag was removed immediately after sampling and sealed in a plastic bag. The venturi suction method resulted in loss of meiofaunal animals (< 0.5 mm body size) through the mesh bag.

Samples of microhabitats and associated epifauna were taken to the surface and preserved in the field. All samples, except those of live corals, were fixed immediately in 5% buffered formalin solution. Live coral samples were rinsed three times in fresh water to remove animals, which were then fixed in 5% buffered formalin solution. A previous study showed no significant differences in abundance of epifauna removed from microhabitats fixed immediately in 5% formalin compared with those rinsed three times in fresh water (Fraser et al. 2020a).

Samples were transported to laboratory facilities and, once fixed, epifauna were removed from their habitat using a jet of fresh water and by shaking in a bucket. Epifauna were collected on a 125 μm sieve and stored in 70% ethanol:2% glycerol:28% water solution for up to 12 months before processing.

Concurrent with sample collection, 20 random photographs of substrata and benthic organisms were taken along a 50 m survey transect through the site. Photographs ('photoquadrats') were taken directly downwards from approximately 50 cm above the seabed to encompass an area of approximately 30 × 30 cm. Photo-quadrats were not available for sites sampled in 2015 (Fig. 1); consequently, photo-quadrats taken from the same sites in the nearest year of surveys (2013) were used to characterise the habitat composition at these sites.

Tropical and temperate biomes divided locations north or south of 30°S, depending on whether reef was dominated by macroalgae (temperate) or coral (tropical) (Malcolm et al. 2010). The Solitary Islands (approximately 30°S) are situated in a tropical-temperate biotone (Malcolm et al. 2010), supporting rocky reef with a combination of macroalgae and a veneer of attached corals (Dalton and Roff 2013). Preliminary analysis indicated that this location grouped with the other temperate locations in non-metric multidimensional scaling (MDS) analysis of the taxonomic composition of sampled assemblages (Supplementary information), so was classified as temperate.

Structural characteristics of sampled microhabitats (Table 2) were assessed, based on characteristics identified by Edgar (1994) and Fraser et al. (2020a) as important for epifaunal community structure. Variation in structural characteristics among habitat groups and biomes was visualised using box plots in R x64 3.6.1 (<www.r-project.org>) using the *tidyverse* package (Wickam et al. 2019).

Laboratory processing

Invertebrates from each sample were washed of formalin and passed through a nested series of 12 sieves stacked in descending order of mesh size, following a $\log_{\sqrt{2}}$ series (8, 5.6, 4.0, 2.8, 2.0, 1.4, 1.0, 0.71, 0.5, 0.355, 0.25, 0.18, 0.125 mm, after Edgar 1990). Invertebrates retained on each sieve were washed into petri dishes, identified and counted under a dissecting microscope, with data binned by sieve mesh size. Identification was performed to order level where possible, otherwise to phylum (< 2% of animals).
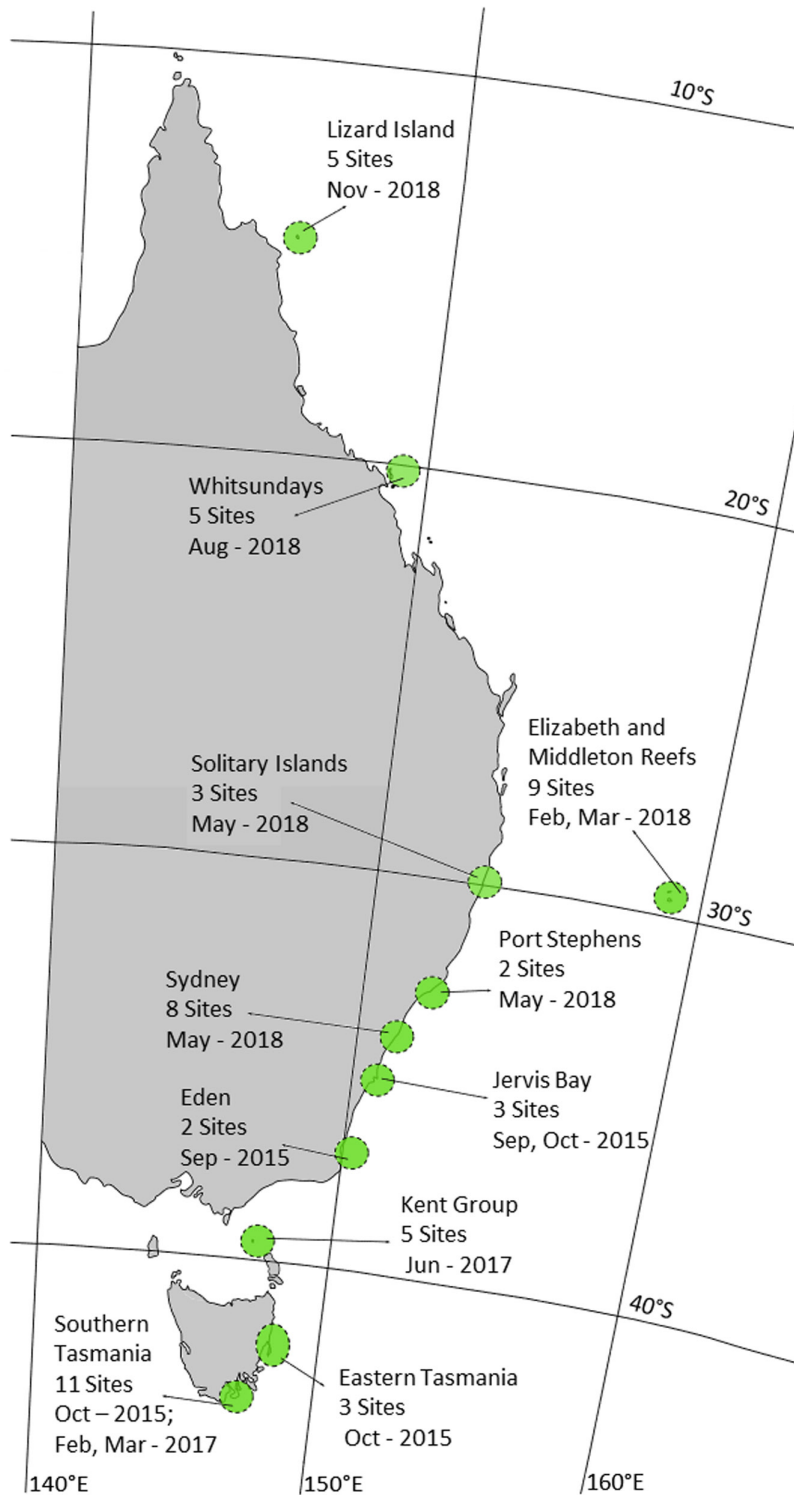
Figure 1. Map of sampling locations showing sampling dates and number of sites.

Data analysis

For each sample collected using the venturi suction method, abundance estimates of smaller animals (< 0.5 mm) were extrapolated by taking the slope and intercept of the linear regression ($\log_{10}$ (abundance + 1) against $\log_{10}$ (sieve mesh size)) for mesh sizes 0.5–2 mm. This extrapolation seemed reasonable given extremely high linearity in abundance/body size relationships for habitats sampled to 0.125 mm sieve body size . The linear regression slope and intercept were used

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Table 1. Microhabitats sampled, with habitat group in which they are nested, description and example genera. The distinction between microhabitats was based on a combination of taxonomy and morphology, as applied in previous studies to classify seabed habitat types (Cresswell et al. 2017) and by the CATAMI scheme (Althaus et al. 2015), which provides a national standard for Australian benthic habitat classification.

Microhabitat	Habitat group	Description	Example genera
Fucoid algae	Macroalgae	Robust, vertical, complex-branching brown algae, leafy appearance	*Sargassum, Xiphophora, Acrocarpia, Cystophora*
Large brown laminarian kelps	Macroalgae	Large habitat forming, overstorey kelp, wide lamina	*Ecklonia, Lessonia*
Small to medium foliose brown algae	Macroalgae	Sheet-like, soft plate-like or filamentous brown understorey algae	*Zonaria, Dictyota, Padina, Lobophora, Halopteris*
Caulerpa	Macroalgae	Green algae of genus *Caulerpa*, thick vertical growth (often finely branching) from horizontal stolon	*Caulerpa*
Foliose green algae	Macroalgae	Thin sheet-like, thick branching or filamentous green algae, vertical growth habit	*Ulva, Codium, Chlorodesmis, Chaetomorpha*
Foliose red algae	Macroalgae	Flexible red algae, branched or leafy, vertical growth habit	*Plocamium, Gracilaria, Pterocladia, Acathophora, Laurencia*
Geniculate coralline algae	Macroalgae	Red calcified algae, fine branches jointed or segmented, vertical growth habit	*Corallina, Amphiroa*
Green calcified algae	Macroalgae	Green algae, branching into calcified segments, prostrate growth habit	*Halimeda*
Turfing algae	Turfing algae	Fine filamentous turfing algae ≤ 2 cm high growing densely or matted on hard substrate, with minimal sandy sediment entrapped	*Feldmannia, Polysiphonia*
Dead coral	Turfing algae	Dead erect coral skeleton overgrown with fine filamentous turfing algae	*Acropora (dead), Pocillopora (dead)*
Coral rubble	Turfing algae	Broken dead coral rubble overgrown with fine filamentous turfing algae	*Acropora (dead), Pocillopora (dead), Porites (dead)*
Soft coral	Sessile invertebrates	Semi-erect, lobed soft corals	*Lobophytum, Sarcophyton, Xenia*
Sponges, encrusting	Sessile invertebrates	Sponges forming a crust over substrate	*Mycale, Aplysilla, Tedania, Chondrilla*
Sponges, erect	Sessile invertebrates	Erect sponges rising from substrate, colony height greater than width, appears solid in cross-section	*Halichondria, Echinoclathria, Ancorina*
Hydrocoral	Live coral	Branching or foliaceous erect colonies	*Millepora*
Massive coral	Live coral	Slow-growing, massive, small polyp stony corals	*Porites*
Pocillopora	Live coral	Stony corals forming branched colonies, genus *Pocillopora*	*Pocillopora*
Branching *Acropora*	Live coral	Stony, branching corals forming colonies, genus *Acropora*	*Acropora*
Tabular *Acropora*	Live coral	Stony branching corals forming tabular colonies	*Acropora*
Other branching/erect coral	Live coral	Fine or robust branching, columnar or foliaceous stony coral colonies	*Porites, Turbinaria, Seriatopora, Stylophora*

to estimate $\log_{10}(\text{abundance}+1)$ for each of the sieves with mesh size < 0.5 mm; data were then back-transformed.

Because strong relationships exist between epifaunal biomass and light irradiance (Edgar 1993), which is a planar metric in relation to the seabed, epifaunal abundance data by size bin were standardised to 1-m² seabed area (Fraser et al. 2020a). Standardisation by seabed area also allowed comparison of epifaunal size spectra data to densities of other trophic groups (e.g. primary producers, benthic invertebrates, fishes), which are typically expressed per square metre of seabed. Moreover, alternative ways of standardising microhabitats generate bias towards species that respond to that particular feature; for example, in the study of 109 common macrofaunal species by Edgar (1983), only 20, 13, 10 and 8 species were significantly associated with epiphyte dry weight, wet algal weight, algal surface area and dry algal weight, respectively.

Data analyses tested variation in epifaunal size spectra in association with microhabitats and habitat groups, and locations and biomes distributed along the latitudinal gradient (Table 3). We found no effect of temperature within biome on size spectra slopes for different microhabitats (ANCOVA; $F = 3.57_{1,50}$, $2.9_{1,48}$; $p = 0.06$, 0.08; for tropical and temperate biomes respectively); consequently, subsequent analyses focused on tropical/temperate comparisons only.

Accounting for habitat variation among sampling locations
The fraction of cover provided by microhabitats was estimated using data derived from photo-quadrat analysis. At each site, size-distribution estimates for all microhabitats were summed to give an estimate of site-level epifaunal density per size bin. Photo-quadrats were assessed to estimate the fraction of cover provided by each microhabitat within a site. Within each site,

Table 2. Microhabitat structural characteristics. Degree of branching ranges from low (1) to high (9). Massive coral maximum height was taken from the entire sampled area; branching was 1. For turfing algae, dead coral and coral rubble maximum height were approximate for turf filaments; turf filaments were generally assigned 1 for degree of branching; degree of branching for dead coral and coral rubble was based on the structure of the coral skeleton.

Characteristic	Description	Range/levels
Maximum height	Height (cm) from base to distal tip of sample	0.2–88 cm
Degree of branching	Complexity metric following (Edgar 1983); analogy derived from stream classification (Horton 1945): order of the primary axis, whenever an axis splits the order increases by one	1–9
Flexibility	Flexibility of microhabitat structure	1 – rigid 2 – semi-rigid 3 – semi-flexible 4 – flexible

95% of the cover of living benthic microhabitats was represented by microhabitats from Table 1.

For each site, the proportional cover of each microhabitat was multiplied by the density of epifauna in each size bin from a sample of the same microhabitat collected from that site. When a microhabitat was recorded in photo-quadrat data but not collected at a given site, epifaunal size distribution data from another site within the same location were used. Microhabitats in photo-quadrat data for which no epifaunal data existed comprised <5% of cover at any site and were omitted from analyses. We assume that this data interpolation would add little error to site estimates because variation between microhabitats within major habitat types at different locations (i.e. microhabitat × location interaction) was low.

The relationship between epifaunal density and size at the site-level was estimated using linear regression in R x64 3.6.1 (<www.r-project.org>) using the *tidyverse* package (Edwards et al. 2017, Wickam et al. 2019), as:

$$\ln(\text{density}) \sim \ln(\text{size})$$

where size is the midpoint of each size bin. The slope of this linear relation was the response of interest (the size spectrum slope). Zeros were treated as missing values as those values were likely to be closer to 0.1 than 0 with further sampling. Variation in slopes between biomes and among locations (nested within biome) was examined using univariate permutational analysis of variance (PERMANOVA; Anderson 2001, 2017, McArdle and Anderson 2001).

Table 3. Factors tested according to their influence on variation in the size spectra of epifaunal assemblages. Nested factors are indicted by parentheses enclosing the factor in which they are nested.

Factor	Fixed/random	No. of levels
Habitat group	Fixed	4
Microhabitat (Habitat group)	Random	20
Biome	Fixed	2
Location (Biome)	Random	11

Assessing the interactive effects of habitat, location and biome on size spectra

Variation in sample-level size spectra slopes among microhabitats, habitat groups, locations and biomes was examined using univariate permutational analysis of variance (PERMANOVA; Anderson 2001, 2017, McArdle and Anderson 2001). The size spectrum slope for each sample was calculated using a linear regression (ln(density) against ln(mid-point of each size bin)) in R (<www.r-project.org>) (Edwards et al. 2017), with zeros treated as missing values. The original tested model included covariates: habitat group, microhabitat (nested within habitat group), biome and location (nested within biome), and all interaction terms. Following Winer et al. (1991), terms for which p > 0.25 were removed from the second tested model, which included: habitat group, microhabitat (habitat group), biome, habitat group × biome, microhabitat (habitat group) × location (biome).

Mean epifaunal size spectra slopes were subsequently estimated for each combination of biome and habitat group. Calculations of size spectra for turf and massive coral microhabitats excluded size bins < 0.5 mm as loss of smaller animals due to suction sampling meant data were inaccurate.

Variation in the density contribution of different taxonomic groups across size spectra, among habitat groups, and between biomes was visualised using R (<www.r-project.org>). Most invertebrates (93%) were crustaceans, so epifauna were subdivided into three taxonomic groups: Decapoda, Peracarida and Harpacticoida, with additional taxa comprising a fourth group 'other invertebrates'. Decapods dominated the largest size bins, peracarids the intermediate and harpacticoids the smallest. Size bins were combined into five groups to more clearly visualize patterns of variation: 0.125–0.18, 0.25–0.355, 0.5–0.71, 1–1.4, 2–2.8 and 4–8 mm.

Results

Size spectra variation among sampling locations

Using site-level estimates of epifaunal density per size bin (i.e. aggregated across the microhabitats observed at each site), neither slopes nor intercepts differed significantly between tropical and temperate biomes (Table 4). Variation in slopes

Table 4. Univariate PERMANOVA assessing effects of biome (tropical or temperate) and location (nested within biome) on the slope and intercept of site-level epifaunal size spectra. Nested factors are indicted by parentheses enclosing the factor in which they are nested. Effects highlighted in bold were significant at alpha < 0.05. Negative values for percentage of variation explained by each factor are recorded as 0.

Source of variation	Degrees of freedom	Mean square	Pseudo-F ratio	p-value (by permutation)	% variation
Size spectrum slope					
Biome	1	0.32	0.40	0.577	0
Location (Biome)	**9**	**0.78**	**5.67**	**0.001**	**53.2**
Residual	33	0.14			46.8
Total	43				
Size spectrum intercept					
Biome	1	5.46	5.35	0.053	36.1
Location (Biome)	**9**	**0.99**	**3.50**	**0.011**	**25.9**
Residual	33	0.28			38.0
Total	43				

among locations (nested within biome) was, however, significant (Table 4). In order to visualise the differences between locations, the slopes of location-level plots of size spectra, which were compiled using the mean epifaunal density in each size bin across sites within locations, were highly linear with extremely good fits ($R^2 > 0.8$; Fig. 2). A slight deviation from this log-linear pattern was observed in southern Tasmania, however a relatively high R^2 value (0.81) justified plotting these data using a linear model for ease of comparison with other locations.

Interactions between habitat, location and biome

No significant variation in size spectra slopes was evident between microhabitats within habitat groups (Table 5), but slopes differed among the broader habitat groups (Table 6). Size spectra slopes were linear with a good fit ($R^2 = 0.60$–0.83) for all combinations of habitat group and biome, except for tropical live coral ($R^2 = 0.37$) (Fig. 3a). PERMANOVA indicated a significant interaction between habitat group and biome (Table 6), suggesting tropical-temperate variation in size spectra slopes differed between habitat groups. Variation in structural characteristics among habitat groups and between biomes was assessed to help clarify possible reasons for temperate and tropical size spectra differing for some habitat types (Fig. 3b–d). Notably, components of variation for all assessed factors were less than for residual error, indicating that none of the assessed factors greatly affected slope relative to unaccounted variability.

Shifts in community composition along size spectra largely reflected changes in major crustacean groups – the dominant epifaunal taxa (Fig. 4). Harpacticoid copepods were the major contributors to the smallest size bins across all habitat groups, reaching highest proportions in the tropical biome. Peracarids were prevalent across a broad size range on macroalgae, particularly within the temperate biome. Peracarids were also important across a broad size range on the turf habitat group, whereas on sessile invertebrate and live coral habitat groups peracarids were most abundant in a reduced size range (0.5–2.8 mm on sessile invertebrates and 1–1.4 mm on live coral). Decapods dominated the largest size groups on the live coral habitat group with notable presence in the tropical biome, where they contributed most density from 2

to 8 mm. The 'other invertebrates' group tended to be more prevalent within the temperate biome, with a contribution that varied among size groups and habitat groups.

Discussion

The community size spectrum for epifaunal invertebrates inhabiting eastern Australia's shallow reefs was remarkably consistent and linear when aggregated across observed local microhabitat mosaics at the scale of 50 m transects and plotted on a log–log scale. Comparing these estimates of epifaunal size spectra that accounted for local habitat variation, no latitudinal pattern was apparent among reef locations across a substantial biogeographic gradient. Within each location, a linear model explained variation remarkably well ($R^2 \geq 0.8$). Similarly, size spectra were consistently linear (with one exception) when plotted among structurally heterogenous habitat groups ($R^2 \geq 0.6$). The results presented here support the hypothesis that epifaunal assemblage size spectra vary as a result of interactions between habitat type and climatic zone, since observed variation in size spectra between tropical and temperate biomes depended on the habitat group from which epifauna were collected. This suggests that any shifts in size spectra at this basal level of reef food webs, due to continuing climate change, will be predominantly mediated via changes in the availability of benthic habitats.

Habitat and size spectra variation

Epifaunal size spectra varied among habitat groups, eclipsing any tropical/temperate variation. When mean size spectra were estimated at the location level using proportional microhabitat cover at sampling sites, variation among locations reflected variation in microhabitat cover. The lack of biome effect suggested these differences in cover were more influential than environmental differences broadly associated with biomes.

A strong influence of habitat is unsurprising, given habitat structure at the scale appropriate to small epifaunal invertebrates has been identified as an important correlate of assemblage composition (Hacker and Steneck 1990, Gee and Warwick 1994, Chemello and Milazzo 2002, Stella et al.
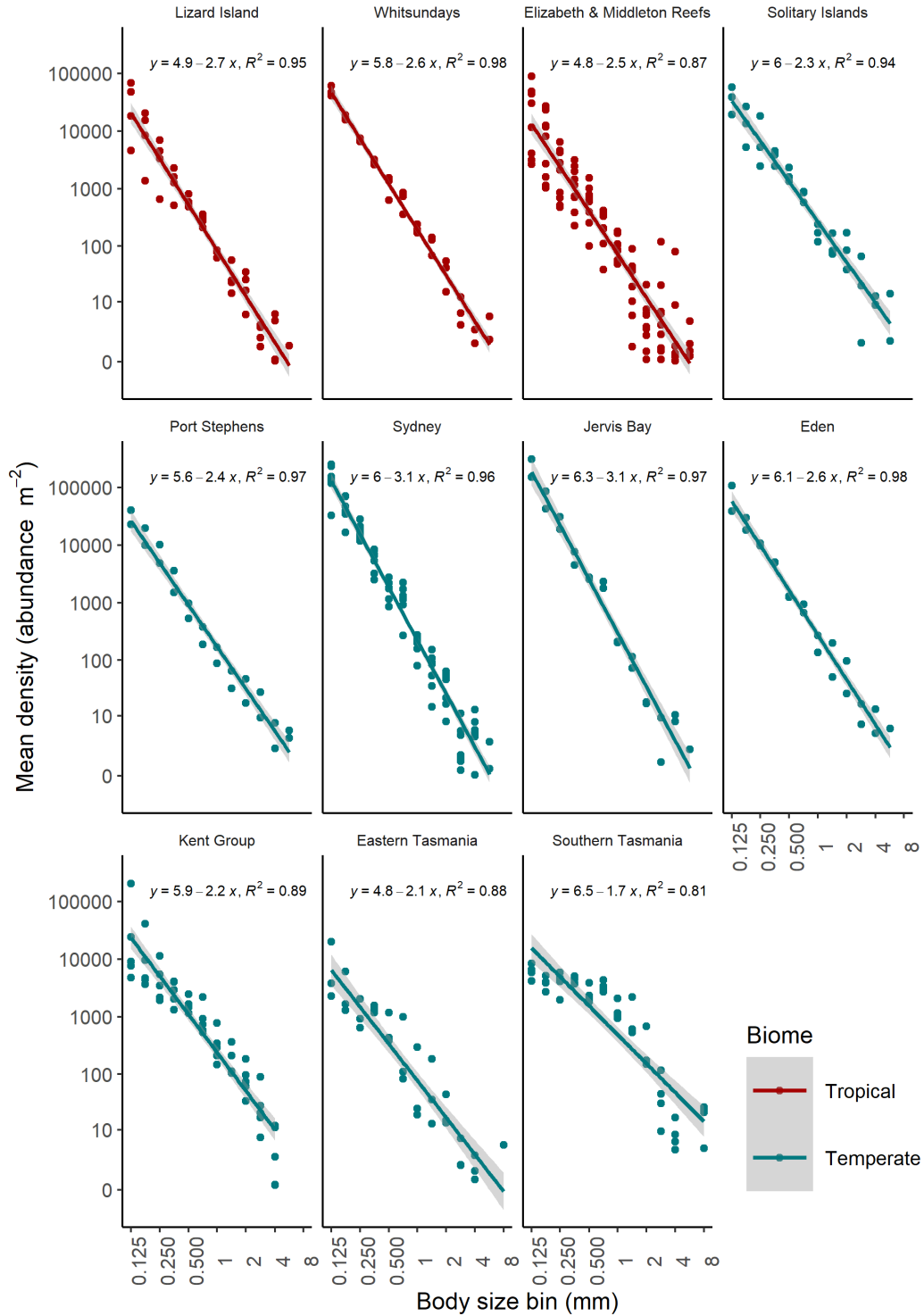
Figure 2. Size spectra relating mean density (ln(density) against ln(size bin mid-point)) of epifauna for each sampling location, estimated by summing proportional cover of benthic microhabitats at each site. Locations are arranged left to right from lowest to highest latitude. Points represent density estimates within a size bin for individual sites, grey shading represents 95% confidence intervals. Y-axis breaks are presented on a $\log_{10}$ scale rather than $\log_e$ scale for ease of interpretation.

2010, Kramer et al. 2014, Marzinelli et al. 2014, Fraser et al. 2020a, Stelling-Wood et al. 2020). Despite the habitat-driven variation observed in epifaunal size spectra, both site- and sample-level size spectra were highly linear and, as

expected, negatively sloped (Peters and Wassenberg 1983, Marquet et al. 1990). With one exception (described below), all size spectra closely fit a linear model ($R^2 \geq 0.6$). This suggests that, if given a small size range of invertebrates in a

Table 5. Univariate PERMANOVA assessing effects of habitat group, biome (tropical or temperate), microhabitat (habitat group), location (biome) and all interaction terms on the slope of sample-level epifaunal size spectra. Nested factors are indicted by parentheses enclosing the factor in which they are nested. Effects highlighted in bold were retained in the final model at alpha < 0.25. Negative values for percentage of variation explained by each factor are recorded as 0.

Source of variation	df	Mean square	Pseudo-F ratio	p-value (by permutation)	% variation
Habitat group	**3**	**1.90**	**2.82**	**0.044**	**18.8**
Microhabitat (Habitat group)	**17**	**0.71**	**1.31**	**0.238**	**4.7**
Biome	**1**	**1.21**	**2.00**	**0.169**	**8.3**
Location (Biome)	9	0.54	0.97	0.509	0
Habitat group × Biome	**3**	**1.34**	**1.82**	**0.124**	**5.0**
Microhabitat (Habitat group) × Biome	7	0.69	1.33	0.270	20.7
Habitat group × Location (Biome)	11	0.55	1.04	0.447	0.6
Microhabitat (Habitat group) × Location (Biome)	**25**	**0.56**	**1.53**	**0.109**	**9.4**
Residual	75	0.36			32.5
Total	151				

sample, accurate prediction of invertebrate density in much smaller or larger size classes is possible.

The observed linearity and negative slope of epifaunal size spectra may be explained by metabolic rate scaling with body size. Herbivores comprise the predominant functional group within epifaunal assemblages, with microphytobenthos an important food source for invertebrates across the size spectrum (Edgar 1993). Kleiber's law states that the metabolic rate of an individual animal relates to the animal's mass by the power of 0.75 (Kleiber 1932). Thus, the rate of resource use (e.g. microphytobenthic food) by an individual is relative to its body mass, and this rate scales with body mass. Although Kleiber's law refers to mass, the same concept can be applied to other metrics of body size, although the exact power ratio may vary (Trebilco et al. 2016). Individuals in smaller size classes will require a smaller amount of food so, assuming sufficient food resources are available, one can expect density to decrease as body size increases (Damuth 1981), often at a scale reciprocal to metabolic rate increase (Damuth 1991). Linear size spectra (log–log scale) are generally observed in oligotrophic ecosystems that have not recently experienced major disturbance (Marquet et al. 2005), as well as eutrophic ecosystems dominated by herbivores (Damuth 1981). Common processes that interfere with expected linearity and slope of size spectra include size-selective predation (Rassoulzadegan and Sheldon 1986, Sheldon et al. 1986), and metabolic inefficiencies in the transfer of energy if individuals in larger size

bins feed upon those in smaller size bins (Lindeman 1942, Trebilco et al. 2013). Hence, a steeper slope may be expected within a trophic group if predators target larger individuals, or if intra-group predation occurs.

Among habitat groups sampled here, the steepest size spectra were observed on macroalgae and turfing algae habitats. Macroalgae- and turfing algae-associated assemblages were characterised by relatively high densities of invertebrates in the smallest size classes and relatively low densities in the largest size classes. Small size classes on these habitats were dominated by harpacticoid copepods, whereas taxonomic contributions to large size classes varied between macroalgae and turf, and tropical and temperate biomes.

Macroalgae thalli often host epiphytic microphytobenthos including diatom-dominated films and fine filamentous algae (Poore et al. 2012), providing substantial food resources for herbivorous epifauna. Turfing algae may be directly consumed by herbivorous epifauna, and turf effectively traps detritus (Connell et al. 2014), providing food for detritivores, another important functional group common in epifaunal assemblages (Kramer et al. 2012). Hence, linear epifaunal size spectra may be expected in association with these habitats. Size-selective predation may also contribute to relatively steep slopes on these habitats. The structure of macroalgae and turfing algae is relatively flexible compared with live coral and sessile invertebrates (Fig. 3d), allowing benthic invertivores to easily penetrate in order to extract larger, visible prey

Table 6. Univariate PERMANOVA assessing effects of terms for which p < 0.25 in Table 4 on the slope of sample-level epifaunal size spectra. Final model included: habitat group, microhabitat (habitat group), biome and interactions habitat group × biome, and microhabitat (habitat group) × location (biome). Nested factors are indicted by parentheses enclosing the factor in which they are nested. Effects highlighted in bold were significant at alpha < 0.05.

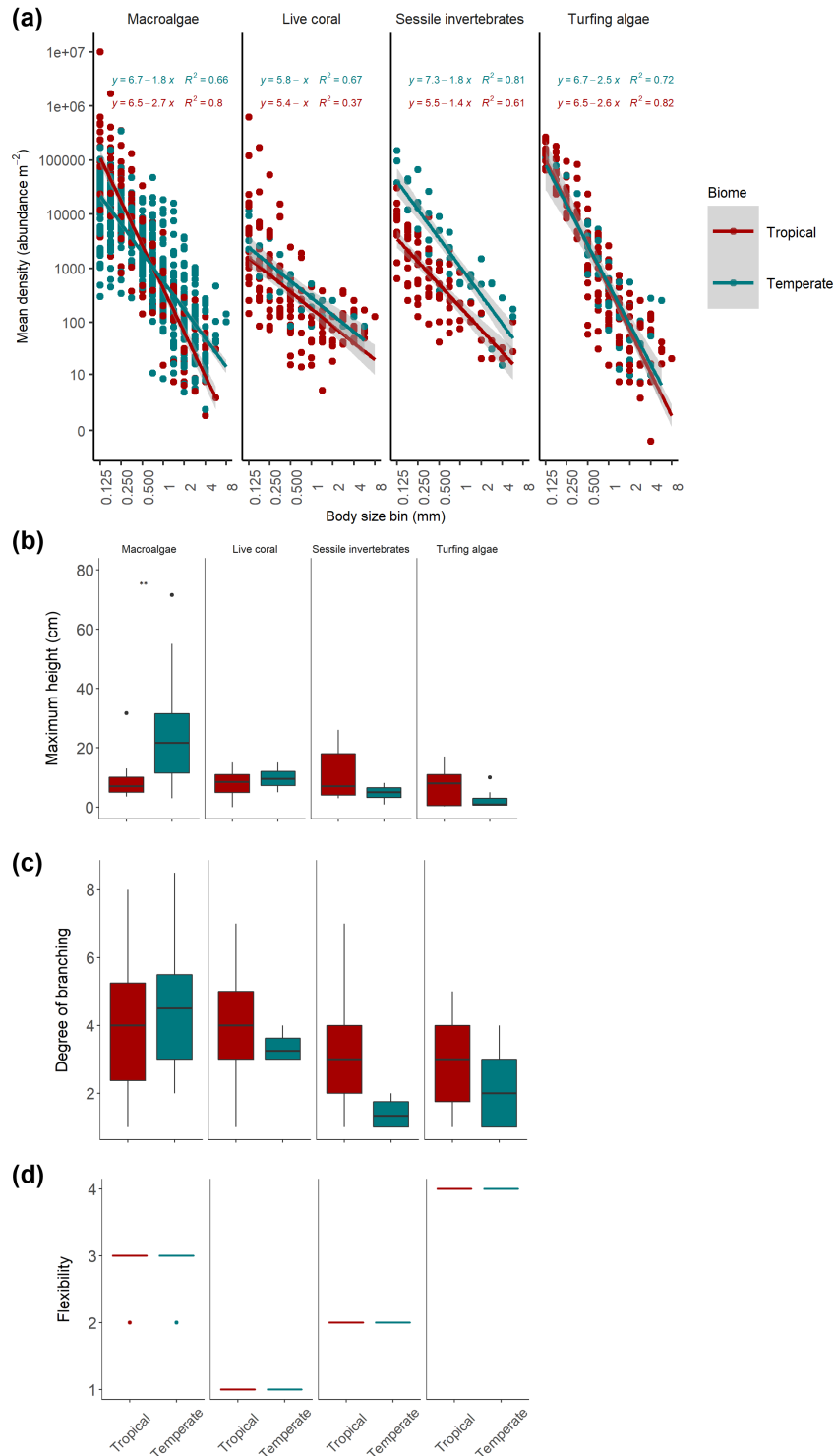| Source of variation	df	Mean square	Pseudo-F ratio	p-value (by permutation)	% variation
Habitat group	**3**	**3.56**	**5.13**	**0.003**	**17.3**
Microhabitat (Habitat group)	17	0.77	1.37	0.220	3.7
Biome	1	1.16	2.13	0.153	2.6
Habitat group × Biome	**3**	**2.52**	**4.55**	**0.016**	**26.3**
Microhabitat (Habitat group) × Location (Biome)	25	0.59	1.32	0.168	6.6
Residual	102	0.44			43.4
Total	151				

Figure 3. Variation among habitat groups and biomes. (a) mean density size spectra of epifauna within each habitat group and biome (ln(density) against ln(size bin mid-point)). Points represent density within a size bin for individual samples, grey shading represents 95% confidence intervals. Density by size data for turf and massive coral microhabitats (within habitat groups turfing algae and live coral, respectively) excluded animals <0.5 mm due to inaccurate sampling by suction. y-axis breaks are presented on a $\log_{10}$ scale rather than $\log_e$ scale for ease of interpretation. Box plots of variation in (b) maximum height (cm), (c) degree of branching and (d) relative flexibility among habitat groups and tropical and temperate biomes. Horizontal lines in each box plot represent, from top to bottom, third quartile, median and first quartile. The end of the top whisker represents the maximum (extending ≤1.5× interquartile range (IQR)), the end of the bottom whisker represents the minimum (extending ≤1.5 × IQR). Dots represent outliers. Asterisks indicate significant tropical/temperate differences (0.01 < p < 0.001).
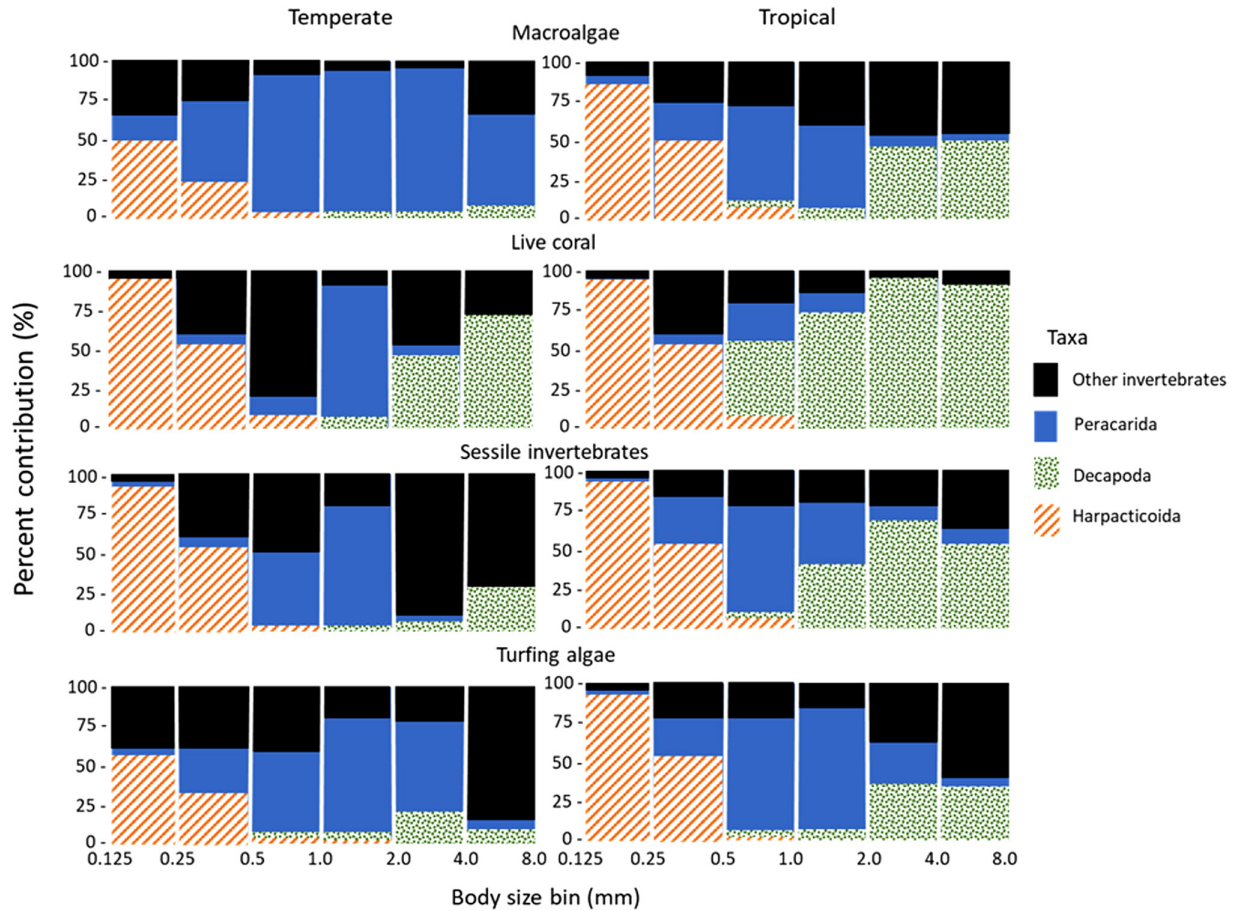
Figure 4. Percent contribution of four taxonomic groups (Decapoda, Peracarida, Harpacticoida and 'other invertebrates') to epifaunal density among size bins according to habitat group and biome.

items (Hixon and Jones 2005). The presence of micro-carnivores within these epifaunal assemblages may also influence the slope, but the functional composition of assemblages has not been considered here.

By contrast, live coral-associated assemblages showed much flatter size spectra than the algal habitat groups, with considerably lower invertebrate densities in the smallest size classes and marginally higher densities in the largest size classes. Harpacticoid copepods comprised >90% of epifauna in the smallest size classes on live coral, with decapods dominating the largest size classes. Predation by large epifauna on animals in smaller size bins is less likely on live coral than on algal habitats, given the lower size spectrum intercept observed on these habitats (Lindeman 1942, Trebilco et al. 2013).

Epifauna on sessile invertebrate habitats possessed size spectra that generally fell mid-way between algal habitats and live coral, with relatively high invertebrate densities in the largest size classes and moderate densities in the smallest size classes. As was the case for live coral habitats, the smallest size classes on sessile invertebrate habitats comprised > 90% harpacticoid copepods with the largest size classes dominated by decapods in tropical samples and the 'other invertebrates' group in temperate samples.

As well as possessing flatter size spectra, epifaunal assemblages inhabiting tropical live coral represented an exception to size spectra linearity (Fig. 3a; $R^2 = 0.37$). This suggests the live coral habitat group is favourable to particular epifaunal size classes. With the exception of massive corals, it is likely that the rigid, often complex structure of live coral limits predator access to epifauna, providing size-dependent refuge for larger invertebrates (Kramer et al. 2016). Predation by corals may also partly explain the lower densities of small epifauna on live coral, as coral polyps can consume very small invertebrates (Goreau et al. 1971, Gochfeld 2004, Houlbréque and Ferrier-Pagés 2009). Some larger decapods consume food resources directly associated with live coral, such as coral mucus or particles trapped by coral polyps (Galil 1987), making live coral habitat preferable to these animals. By contrast, live coral habitat offers minimal microphytobenthic food to herbivorous epifauna (Yamashiro et al. 2012), which may influence the relative paucity of small and mid-sized invertebrates in these assemblages (Edgar 1993).

The predictable relationship between habitat group and epifaunal size spectra provides useful information for estimates of size spectra shifts in response to reef habitat transformation. If benthic habitat availability can be accurately mapped and changes documented or predicted, the availability and

size structure of the epifaunal food source within reef food webs may be estimated, with consideration of the habitat group × biome interaction adding further accuracy.

Interactive influences of habitat and climate

The interaction between the effects of habitat and biome on size spectra slopes suggested temperate-tropical differences among samples in the macroalgal and sessile invertebrate habitat groups (Fig. 3a). Epifauna associated with macroalgae from tropical reefs had a steeper assemblage size spectrum than those from the same habitat group from temperate reefs. In fact, the size spectrum of epifauna on tropical macroalgae was most similar to the epifaunal size spectrum of tropical turf samples. Epifaunal size spectra slopes in sessile invertebrate habitats were slightly steeper in temperate samples, and epifaunal densities also tended to be higher across size classes.

On one hand, size spectra differences between temperate and tropical samples for these broader habitat groups could be confounded by temperate-tropical differences in the microhabitats that make up the broader habitat. For example, the sessile invertebrate habitat included a combination of soft corals and sponges, with samples from tropical reefs comprising 57% soft coral and 43% sponges, whereas 100% of samples from temperate reefs in this habitat group comprised sponge microhabitats. Likewise, large laminarian kelps only contributed to the macroalgal habitat in temperate samples. Such confounding is unlikely to be solely responsible for the significant interaction, however, as the non-significant effect of microhabitat on size spectra slopes (Table 5, 6) suggests that epifaunal size spectra did not vary significantly between soft corals and sponges or the various macroalgal microhabitats.

Instead, structural differences between the microhabitats sampled in the temperate and tropical locations appear to provide a more direct explanation, probably mediated by variation (albeit non-significant) between microhabitats. Macroalgal samples collected from temperate reefs were taller and more branched than tropical macroalgal samples, likely supporting more large epifauna through reduced exposure to predators (and consequently reduced small epifauna through resource constraints) (Edgar 1994). In contrast to macroalgae, sessile invertebrate microhabitats were shorter on temperate reefs, hosting epifauna with a steeper assemblage size spectrum than on tropical reefs. Similar slopes of epifauna in tropical macroalgae and tropical turfs were also reflected in similarities in the degree of branching and height between macroalgae and turfs from tropical reefs, further suggesting that microhabitat height may be an important influence on epifaunal size structure. Tropical/temperate differences in size spectra slopes on select habitats may also be related to variation in the trophic status of reef ecosystems (Sprules and Munawar 1986), assuming tropical reefs sampled here were generally more oligotrophic, and temperate reefs more eutrophic (McClanahan et al. 2002, Burkepile and Hay 2006). Theoretically, in eutrophic systems, nutrients enter the food web at a high rate and are cycled rapidly through grazers in smaller size classes to produce relatively high densities in larger size classes. In oligotrophic systems, by contrast, nutrients enter the food web at a lower rate and slower cycling through small grazers produces fewer grazers in larger size classes (Sprules and Munawar 1986).

Notably, a large residual error remained in both site- and sample-level analyses after accounting for the variation associated with tested covariates and their interactions (Table 4, 6). This may be a product of unexplained ecological or environmental factors that a priori were not considered important, such as biomass of benthic predators or habitat transforming taxa (e.g. herbivores or corallivores), depth, wave exposure or human impacts. The large residual error may also be a result of stochastic noise in the data, due to the broad biogeographic study area and opportunistic sampling approach. Of great overarching significance, however, is that the size spectrum apparently represents an emergent macro-ecological property that is not greatly affected by local environmental factors. Regardless, a sufficiently strong signal exists to assume habitat influences epifaunal size spectra, and that tropical/temperate variation largely depends on habitat.

Implications for climate change predictions

Globally, reef ecosystems are undergoing dramatic changes, with widespread transformation of benthic habitats. Given the clear correlation between epifaunal size spectra and structurally diverse habitats, and the size-specific predation of many benthic invertivores (Edgar and Aoki 1993, Kramer et al. 2015), ongoing shifts in available reef habitats are likely to substantially influence basal food web dynamics. The epifaunal size spectrum on coral-dominated reefs will likely steepen following decline in live coral and increased cover of turf algae and/or macroalgae habitats (Mumby et al. 2007, Nelson et al. 2016, O'Brien and Scheibling 2018), with less food available for invertivores favouring larger decapods and considerably more food available for those favouring small harpacticoid copepods and mid-sized peracarids. In contrast, if reefs historically dominated by macroalgae transform towards higher cover of turfing algae (Filbee-Dexter and Wernberg 2018, O'Brien and Scheibling 2018, Reeves et al. 2018), epifaunal size spectra may not change much. This suggests resource availability for benthic invertivores may be maintained on temperate reefs assuming succession towards turfing algae. If, however, substantial cover of live coral succeeds macroalgae, as described by Ling et al. (2018), epifaunal size spectra may flatten significantly, with dramatic declines in small harpacticoid copepod prey. Increased availability of larger decapod prey may be less widespread in this scenario, depending on the complexity of live corals and subsequent refugia for larger epifauna.

Body-size distribution is often overlooked in studies of community structure, with comparisons of faunal diversity, taxonomic composition, density and biomass more common (Berthelsen et al. 2015, Cúrdia et al. 2015, Desmond et al. 2018). However, results presented here reveal highly predictable properties with regards to the size spectra of epifaunal assemblages on diverse benthic habitats. Without

consideration of size spectra, comparisons of total density or biomass of epifauna would be confounded and largely meaningless, as outcomes would vary considerably depending on the size of animals sampled. For example, using data presented here, density comparisons of epifauna ≥ 1 mm body size between macroalgae and live coral habitat groups will draw opposite conclusions to the same comparison using epifauna < 1 mm (Fig. 3a).

Given the crucial role epifaunal invertebrates play in shallow reef food webs and the assumption that predation patterns vary with epifaunal body size (Edgar and Aoki 1993, Kramer et al. 2015), consideration of epifaunal size spectra is fundamental for understanding potential changes at basal levels of reef food webs as reef habitats transform. The critical nature of information provided by size spectra data likely extends to studies of other faunal communities. For example, comparisons of total fish density inside and outside marine reserves may produce contradictory results, depending on the distribution of body sizes. Thus, results presented here highlight faunal size spectra as an important consideration in future ecological research, particularly for research involving food web dynamics.

Data availability statement

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.5tb2rbp2w> (Fraser et al. 2020b).

Author contributions

Kate Fraser: Conceptualization (supporting); Data curation (lead); Formal analysis (lead); Investigation (equal); Methodology (equal); Project administration (equal); Writing – original draft (lead); Writing – review and editing (equal). **Rick Stuart-Smith**: Conceptualization (supporting); Formal analysis (equal); Investigation (equal); Methodology (equal); Writing – review and editing (equal). **Scott Ling**: Conceptualization (supporting); Data curation (supporting); Formal analysis (equal); Methodology (equal); Writing – review and editing (equal). **Graham Edgar**: Conceptualization (lead); Data curation (supporting); Formal analysis (equal); Funding acquisition (lead); Methodology (equal); Writing – review and editing (lead).

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